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Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology

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Abstract The recent increase in the Atlantic coast population of striped bass, *Morone saxatilis* (Walbaum), prompted managers to re-evaluate their predatory impact. Published and unpublished diet data for striped bass on the Atlantic Coast of North America were examined for geographical, ontogenetic and seasonal patterns in the diet and to assess diet for this species. Diets of young-of-the-year (YOY) striped bass were similar across the Upper Atlantic (UPATL), Chesapeake and Delaware Bays (CBDEL) and North Carolina (NCARO) areas of the Atlantic coast where either fish or mysid shrimp dominate the diet. For age one and older striped bass, cluster analysis partitioned diets based on predominance of either Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), characteristic of striped bass from the CBDEL and NCARO regions, or non-menhaden fishes or invertebrates, characteristic of fish from the UPATL, in the diet. The predominance of invertebrates in the diets of striped bass in the UPATL region can be attributed to the absence of several important species groups in Northern waters, particularly sciaenid fishes, and to the sporadic occurrences of Atlantic menhaden to UPATL waters. In all regions, across most seasons and in most size classes of striped bass, the clupeiod fishes; menhaden, anchovies (*Anchoa* spp.) and river herrings (*Alosa* spp,) and Atlantic herring, *Clupea harengus* L., dominated the diets of striped bass above the first year of life.

KEYWORDS: diet composition, feeding habits, *Morone saxatilis*, striped bass.

Introduction

While the restoration of striped bass, *Morone saxatilis* (Walbaum), represents a landmark success story in marine fisheries management (Field 1997), the restored population brings with it new management issues concerning the predatory impact and forage demands of this increased population of large predators. Although the diet of striped bass on the Atlantic coast of North America has been well studied (Merriman 1941; Hollis 1952; Trent & Hassler 1966; Dovel 1968; Markle & Grant 1970; Schaefer 1970; Manooch 1973;

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Gardinier & Hoff 1982; Hartman & Brandt 1995a; Rulifson & McKenna 1987; Walter 1999; Overton, May, Griffin & Margraf 2000; Griffin 2001), spatial, temporal and methodological differences between studies make comparative assessment of the diet difficult.

Individual diet studies can only sample a narrow geographical or temporal window and rarely can a single study capture the annual diet of migratory segments of the population (Cortes 1997). Furthermore, differences in the method of quantification, sample partitioning, and presentation make it difficult to synthesise this information without access to the raw data. Standardised diet compositions (Cortes 1999) provide a rapid means to synthesise data from multiple quantitative dietary studies by using a weighted average that accounts for sample size in each study. It can be used with several diet assessment methods, such as frequency of occurrence (%F), numerical (%N), mass or volume (%W, %V), reconstructed weight (%$W_{\text{reconstructed}}$) or with compound indices such as an index of relative importance (%IRI). While differences in the method of diet quantification can affect the conclusions from a diet study, different methods often provide similar results suggesting a redundancy in multiple measurements (Macdonald & Green 1983) and justifying the pooling of diets using the standardised diet composition.

The growing interest in the development of multispecies fisheries management plans and the application of ecosystem modeling for fisheries investigations has resulted in a need for synthesised quantitative food habit data, particularly for upper level predatory species such as striped bass (Whipple, Link, Garrison & Fogarty 2000). Individual diet studies provide local information but, when examining the predatory impact of an eightfold increase in the coastal population of striped bass, there is a need for information integrated across the population range. The objectives of this paper are to synthesise available dietary information on striped bass along its coastal range on the Atlantic Coast of North America, construct a standardised diet for striped bass, and examine important seasonal, spatial and ontogenetic themes in the diet conserved across published studies and unpublished raw data.

Materials and methods

Diet information for young-of-the-year (YOY) and age one and older striped bass was obtained from both published and unpublished sources (Tables 1 & 2). Quantitative data from published studies were extracted from tables and the method of quantification dictated how the data were examined.

An index of standardised diet composition was calculated as the proportion that each prey category P_j contributes to the diet weighted by the number of samples:

$$P_j = \sum_{i=1}^{n} P_{ij}N_i \Bigg/ \sum_{j=1}^{m} \left(\sum_{i=1}^{n} P_{ij}N_i \right)$$

where P_{ij} is the proportion of prey category j in study i, N_i the number of stomachs with food used to calculate P_{ij} in study i, n the number of studies, m the number of prey categories and $\sum P_{ij} = 1$ (Cortes 1999). The P_{ij} values were calculated according to the methods used in the original studies with the same ranking criteria employed by Cortes (1999): compound indices (IRI, %IRI) were used preferentially, if available, or single indices (%N, %W, %$W_{\text{reconstructed}}$ %F,

Table 1. Summary of published and unpublished diet studies utilised in this analysis for young-of-the-year (YOY) striped bass. Method indicates the manner which the diet was quantified. *F* represents percent frequency of occurrence, *N* percent by number, *W* percent by weight, and *V* percent by volume

Source	Location	Method	Size range (mm)	*N*	% Empty	Primary prey
Bason (1971)	Delaware River DE	*F*, *N*	25–100	371	26.7	Mysids, amphipods, fish
Boynton *et al.* (1981)	Potomac River MD	*W*	25–100	703	36	Insects, amphipods, mysids
Cooper *et al.* (1998)	Albemarle Sound NC	*N*	30–110	467	9.7	Mysids, copepods, cladocerans
de Sylva *et al.* (1962)	Delaware River DE	*F*	4–150	279	9.3	Mysids, amphipods, *Crangon septemspinosa* (S.)
Gardinier & Hoff (1982)	Hudson River NY	*F*	0–150	273	17.9	Amphipods, fish, copepods
Hartman & Brandt (1995a)	Chesapeake Bay	*W*	N/A	293	N/A	Fish, polychaetes, amphipods
Markle & Grant (1970)	York, Rappahannock, James River VA	*F*, *V*	30–110	331	10.3	Fish, *Crangon septemspinosa* (S.), mysids
Robichaud-LeBlanc *et al.* (1997)	Miramichi River NB	*F*, *N*, *W*	65–84	268	23.2	Mysids, C*rangon septemspinosa* (S.), fish
Rudershausen (1994)	James River VA	*F*, *V*, *N*	30–70	188	2.7	Cladocerans, copepods, insects
Rulifson & McKenna (1987)	Bay of Fundy NS	*W*, *F*	69–94	16	0	*Crangon septemspinosa* (S.)

Table 2. Summary of published and unpublished diet studies utilised in this analysis for striped bass age 1 and older. Method indicates the manner which the the diet was quantified. *F* represents percent frequency of occurrence, *N* percent by number, *W* percent by weight, and *V* percent by volume

Source	Location	Method	Size range (mm)	*N*	% Empty	Primary prey
Dew (1988)	Hudson River NY	*F*	400–1050	508	58	Alosines, *Crangon septemspinosa* (S.), *Ammodytes* spp.
Dilday (unpublished data)	Albemarle Sound NC	*W*	248–665	1649	N/A	Menhaden, Sciaenidae, Alosines
Dovel (1968)	Chesapeake Bay	*N*	N/A	240	N/A	Sciaenidae, anchovy, menhaden
Dunning *et al*. (1997)	Hudson River NY	*F*	200–400	178	53	*Crangon*, Alosines, amphipods
Gardinier & Hoff (1982)	Hudson River NY	*F*	200–800 +	380	73	Isopods, white perch, tomcod
Griffin (2001)	Chesapeake Bay	*W*	183–1183	917	N/A	Menhaden, other clupeids, anchovy
Hartman & Brandt (1995a)	Chesapeake Bay	*W*	150–700	929	N/A	Menhaden, anchovy, Sciaenidae
Holland & Yelverton (1973)	Coastal waters NC	*W*	400–1100	102	18	Sciaenidae, anchovy, menhaden
Hollis (1952)	Chesapeake Bay	*F*	400–1000	1157	44	Anchovy, Sciaenidae, menhaden
Manooch (1973)	Albemarle Sound NC	*F*, *N*, *V*	125–714	1094	23	Menhaden, Alosines, anchovy
Mather & Ferry (unpublished data)	Massachusetts Rivers MA	*W*	291–610	258	N/A	Menhaden, *Crangon*, Ammodytes spp.
Merriman (1941)	N/A	N/A	N/A	N/A	N/A	N/A
Nelson, Chase & Stockwell (2003)	Coastal waters MA	*F*, *N*, *V*	311–1156	2503	46	Decapod crabs, menhaden, lobster
Nemerson & Able (unpublished data)	Delaware River NJ	*W*	300–575	41	N/A	Blue crab, mummichog, *Fundulus heteroclitus* (L.), croaker
NMFS (unpublished data)	Chesapeake Bay–New York	*W*	230–880	75	N/A	Clupeidae, isopods, polychaete
NMFS (unpublished data)	Cape Hatteras–Chesapeake Bay	*W*	460–1180	56	N/A	Menhaden, anchovy, polychaete
NMFS (unpublished data)	Nova Scotia–New York	*W*	240–1120	132	N/A	Tonguefish, *Symphurus plagiusa* (L.), Clupeidae, amphipod
Overton *et al*. (unpublished data)	Chesapeake Bay	*W*	107–1157	2703	N/A	Menhaden, gizzard shad, white perch
Oviatt (1977)	Narragansett Bay, Coast RI	*F*	400–1100	202	N/A	Menhaden, *Ammodytes* spp., cancer crab
Raney (1952)	N/A		N/A	N/A	N/A	N/A
Rulifson & McKenna (1987)	Bay of Fundy, NS	*F*, *V*	141–520	62	3	*Crangon*, Gadidae, silversides
Schaefer (1970)	Long Island, NY	*F*, *V*	600–940	367	21	Amphipods, anchovy, Mysidae
Schulze (1996)	Connecticut River, CT	*F*, *N*, *W*	200–1000	646	33	Invertebrates, fishes
Setzler, Boynton, Wood, Zion, Lubbers, Mountford, Frere, Tucker & Mihursky (1980)	N/A		N/A	N/A	N/A	N/A
Trent & Hassler (1966)	Roanoke River, NC	*F*	400–1000	1070	86	Alosidae, *Notemigonus crysoleucas* (Mitchill), *Cyprinidae*
Tupper & Able (2000)	Delaware River NJ	*N*, *V*	212–670	59	N/A	Blue crab, *Palaemonetes* spp, *Crangon septemspinosa* (S.)
Walter & Austin (unpublished data)	Chesapeake Bay	*F*, *N*, *W*	458–1151	1225	44	Menhaden, sciaenidae, anchovy

%V) were used. If two single indices were provided, such as %N and %F, these were combined, viz. [%N + %V]/2. Studies with only qualitative data or from which numerical data values could not be obtained were not used in the quantitative portion of this study but are listed in Table 1.

For YOY, striped bass 16 prey categories were used to create standardised diets (Table 1). These prey categories represented pooled taxonomic categories corresponding to functionally or ecologically similar prey species though, in some cases, they corresponded to unique species. Twenty-eight prey categories were used to calculate standardised diets from published and unpublished data for striped bass age one and older, however, only the major prey items. Quantitative data used to construct these figures are available from the primary authors. Diets were partitioned according to the criterion of the original authors, usually along spatial, seasonal or ontogenetic gradients.

Because frequency of occurrence is non-additive, this presented a difficulty when combining prey species within a single study into a general category (e.g. combining spot, *Leiostomus xanthurus* Lecépède, and croaker, *Micropogonius undulatus* (L.), into a sciaenid category). If there is no species overlap in a stomach, then this summed frequency of occurrence is the overall frequency for the pooled group. If the species overlap in the stomachs (e.g. two species are always found together in the stomachs), then the frequency of occurrence is that of the most frequently occurring species. Without the raw data, it is only possible to determine minimum and maximum bounds for the frequency of occurrence for a pooled species group between that of the most frequently occurring species in the summed group and the sum of all frequencies of occurrence for the species comprising the species group. The true frequency of occurrence, a pooled frequency that is the midpoint between the most frequently occurring species and the sum of all frequencies of occurrence was given by $(\%\ F_{max} + \%F_{sum})/2$, where $\%F_{max}$ is the maximum frequency of occurrence for any species comprising the pooled group and $\%F_{sum}$ is the sum of all frequency of occurrences for all species in that group. Frequency of occurrence data also present a problem of not summing to a total of 100%, complicating comparisons between $\%N$ and $\%W$. To facilitate pooling of different studies, the $\%F$ data were standardised so that the totals for a given study sum to 100% by summing all $\%F$ and dividing individual species group values by the total $\%F$.

For larger striped bass, diet data were pooled with standardised diets obtained from individual studies and partitioned by size classes and seasons in the three regions (Fig. 1): Upper Atlantic (UPATL), Chesapeake and Delaware Bays (CBDEL) and North Carolina (NCARO). For the unpublished studies, raw data were used as it facilitated partitioning of individual fish to combinations of size, season and location. The first size class (150–450 mm total length) consisted primarily of estuarine resident juveniles and young mature fish aged 1–3, although some of these fish, particularly females, migrate (Merriman 1941). The second size class (451–600 mm) consisted of both resident and migratory fish aged 4–6 and the largest size class (601–1200 mm) consisted of fish assumed to be coastal migrants older than age 6. In the upper Atlantic region, data obtained from Schaefer (1970), Oviatt (1977), Gardinier & Hoff (1982), Rulifson & McKenna (1987), Dew (1988), Dunning, Waldman,

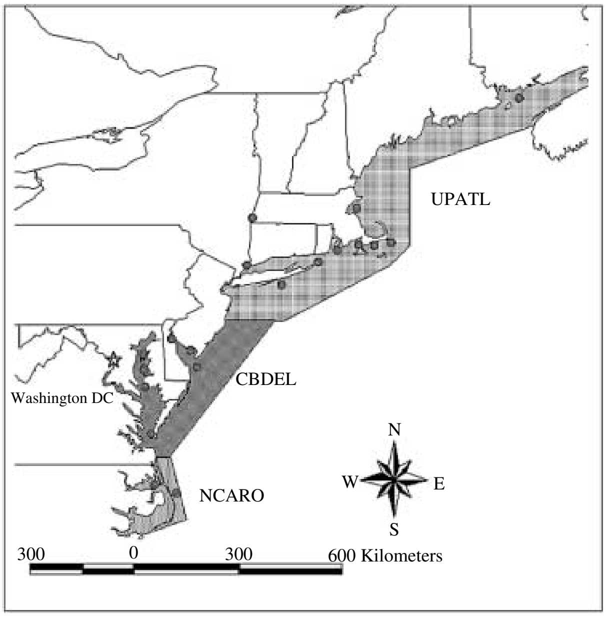

Figure 1. Map of the sampled areas from the striped bass diet. The shaded regions represent the three locations Upper Atlantic (UPATL), Chesapeake and Delaware (CBDEL) and North Carolina (NCARO). Circles represent locations for studies used in this analysis.

Ross & Mattson (1997) and unpublished data sets provided by Mather & Ferry and National Marine Fisheries Service (NMFS) were used to create seasonal and size-specific diets. The size partitioning of fish includes some size overlap where it was difficult to separate pooled data into the three distinct size categories. For the Chesapeake–Delaware region, raw unpublished data provided by Griffin (2001), Nemerson & Able, NMFS, Overton and Walter & Austin, were combined with published data from Hollis (1952) and Hartman & Brandt (1995a), and for the North Carolina region, the data sets provided by Dilday (unpublished data) and NMFS and the studies of Holland & Yelverton (1973) and Manooch (1973) were employed; however, the lack of size class resolution in the data for the North Carolina area precluded partitioning the data by size.

Exploratory partitioning of both the YOY and the larger striped bass studies was conducted by hierarchical cluster analysis (Waite 2000). Cluster analysis using a squared Euclidean distance measure and complete linkage was conducted on the diet composition data using the Minitab statistical package (Minitab, Inc).

Results

Ten studies of YOY striped bass, representing 3273 total fish and 28 adult studies representing 16 553 total

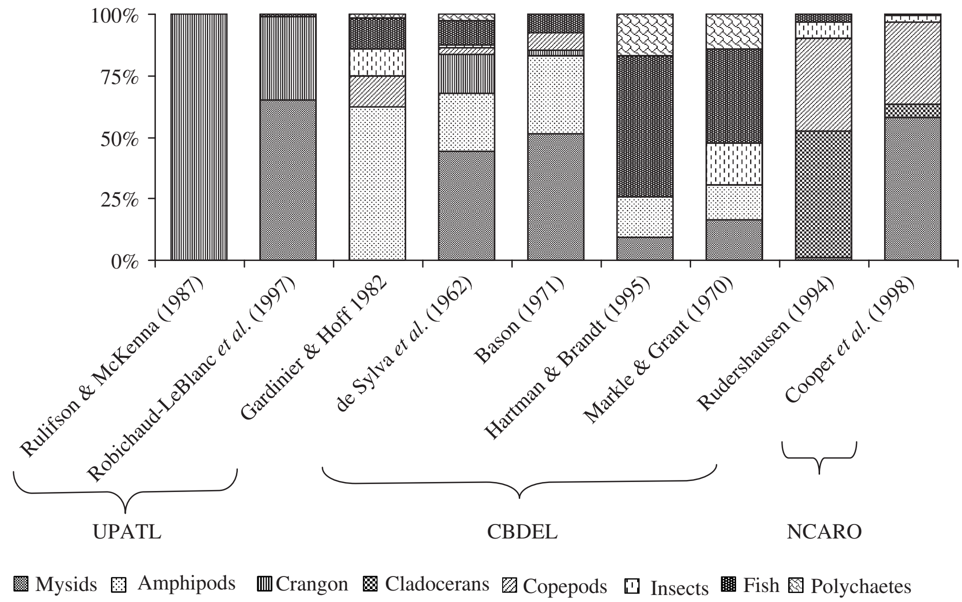

Figure 2. Percentage of major prey of YOY striped bass from individual studies. The studies are arranged in order of decreasing latitude.

fish were used. The geographical coverage ranged from Cape Hatteras, NC to the Miramichi River, New Brunswick and spanned the years 1938–2001.

YOY striped bass

Studies on YOY (Table 1 and Fig. 2) were conducted primarily in estuarine nursery areas where invertebrates dominated the diet, and the inclusion of fish in the diet increased with ontogeny. Clustering of the standardised diets for individual studies indicated little broad-scale regional variation in the diet but high variability between different studies conducted within the same watershed (Fig. 3).

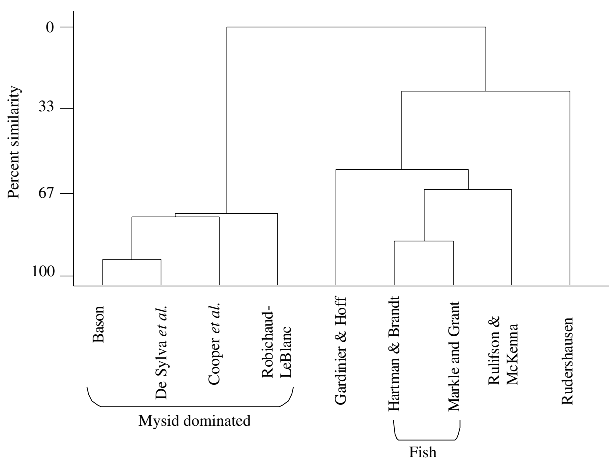

Figure 3. Dendrogram from hierarchical agglomerative cluster analysis of the standardised diet compositions for young-of-the-year (YOY) striped bass.

Rudershausen (1994) found YOY consumed predominantly freshwater zooplankton, Hartman & Brandt (1995a) and Markle & Grant (1970) found higher amounts of fish and benthic crustaceans (Fig. 3). In contrast, Bason (1971), de Sylva, Kalber & Shuster (1962), Cooper, Rulifson, Isley & Winslow (1998) and Robichaud-LeBlanc, Courtenay & Hanson (1997), covering the North Carolina to Bay of Fundy, NS, area all found mysid shrimp, primarily, *Neomysis americana* (Smith), the predominant prey species.

The absence of across-region variability in the diets and the high variability even within a watershed reflect the spatial and ontogenetic variation in trophic ecology of YOY striped bass. YOY striped bass hatch in tidal freshwater rivers and spend their first year of life in the brackish estuary where the food base is generally similar across their Atlantic coast distribution. However, within a river or estuarine system, the diets vary depending upon spatial location and salinity regime (Markle & Grant 1970; Boynton, Polgar & Zion 1981; Robichaud-Leblanc *et al.* 1997). The low taxonomic diversity of food types in tidal fresh and brackish estuarine waters results in diets that are fairly similar across regions but differ at different locations within an estuary, translating into spatial variation in growth rates and trophic position (Wainright, Fuller, Michener & Richards 1996).

Ontogenetic variation in the diet within the first year was observed by Robichaud-Leblanc *et al.* (1997) and

Markle and Grant (1970). Cluster analysis separated fish collected by Rudershausen (1994) (Fig. 3) on the basis of the smaller size range of fish examined (30–70 mm) that fed primarily upon cladocerans, copepods and insects. Robichaud-Leblanc *et al.* (1997) and Cooper *et al.* (1998) found a shift in diet at 50 mm from one dominated by copepods and cladocerans to a diet of decapod crustaceans and mysid shrimp. At sizes of 70–90 mm, both Markle & Grant (1970) and Cooper *et al.* (1998) observed a shift towards greater piscivory. Concomitant with the increase in size is net movement away from the natal tidal fresh water into higher salinity estuarine waters so the ontogenetic changes in diet also reflect spatial variation in the estuary.

Age one and older striped bass

Cluster analysis of the diets of age one and older striped bass between 150–1183 mm grouped studies according to the importance of dominant prey species, primarily whether menhaden was the dominant prey (Fig. 4). Atlantic menhaden account for over 45% of the diet in seven studies and 32% of the overall diet for all studies combined. Four other diet groupings: sciaenid fishes, amphipods, *Crangon septemspinosa* (Say), and other decapod crustaceans, partition the remaining diet studies.

Clustering diet studies into similar groupings based on dominant prey species underscored several important trends. Most notably, invertebrates, primarily decapod crustaceans and gammarid amphipods dominated diets of striped bass in Upper Atlantic waters (Fig. 5). The increased importance of invertebrates in the diets of striped bass in northern waters may partially be a result of the sporadic availability of some clupeid prey and the absence of abundant sciaenid fishes in this region. Mather & Ferry (unpublished data) found that menhaden were the dominant prey in Massachusetts estuaries in years of high abundance; however, Atlantic menhaden recruitment to northern waters occurs later in the year and is more variable than in CBDEL and NCARO (Reintjes & Pacheco 1966). Sciaenid fishes are uncommon in waters in the UPATL region and appear to have been replaced by demersal gadoids, represented by hakes, *Urophycis* spp., and Atlantic tomcod, *Microgadus tomcod* (Walbaum), in diets of striped bass in Northern waters. Similarly, American sand lance, *Ammodytes* spp., appear to replace bay anchovy, *Anchoa mitchilli* (Val.), in the diet of fish in Northern waters. Both sand eels and bay anchovy are a primary small forage species in the areas where they occur.

Regional diet differences

Upper Atlantic region. In the Upper Atlantic region, several seasonal and ontogenetic patterns were evident (Fig. 6). The diets of all size classes of striped bass

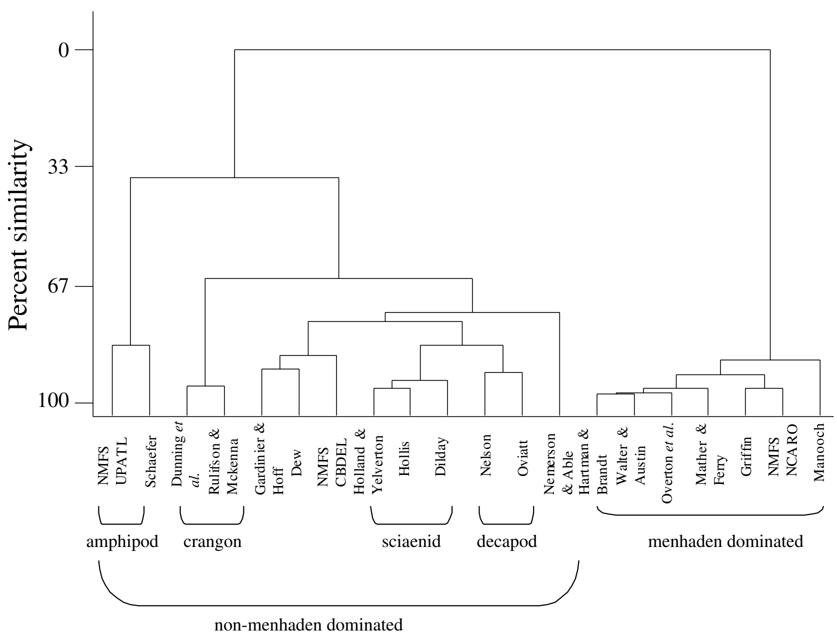

Figure 4. Dendrogram from hierarchical agglomerative cluster analysis of the standardised diet compositions of striped bass older than young-of-the-year. Labels at the bottom of clusters indicate the groupings based on dominant prey species shared within clusters.

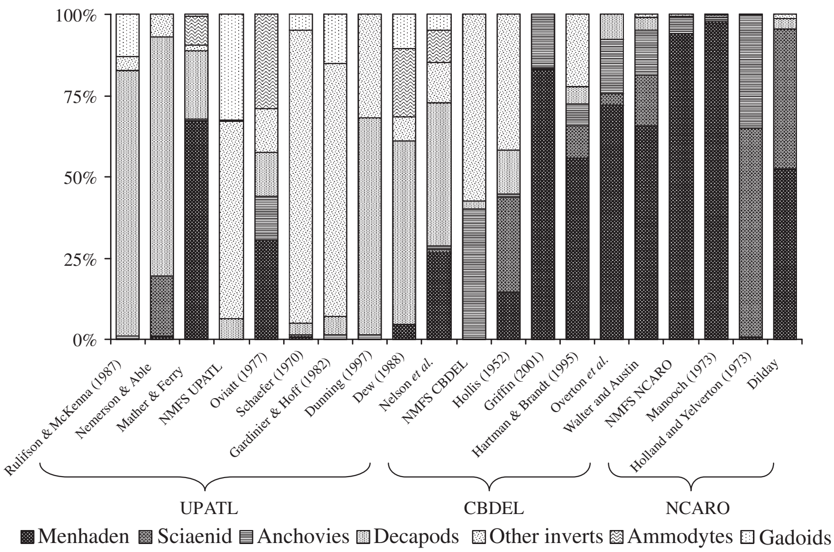

Figure 5. Percentage of major prey of striped bass from individual studies. The studies are arranged in order of decreasing latitude. Sample sizes and size classes are shown in Table 2. No year after an author name indicates that the data are unpublished.

consisted primarily of sand shrimp and amphipods in the spring and summer. Alosines, primarily blueback herring, *Alosa aestivalis* (Mitchill), contributed intermediate amounts to the remainder of the diet in the spring and minor amounts in autumn and winter. Adult blueback herring ascend tributary rivers in spring and represent an abundant and accessible food source for pre- and post-spawning striped bass (Trent & Hassler 1966). Fish began to contribute increasingly to the diets of striped bass through the summer and into the autumn. Atlantic menhaden first appear in the diets in summer when juveniles recruit to UPATL estuaries and adults migrate into these waters. Diets of striped bass in autumn consisted largely of amphipods, however, menhaden, bay anchovy and gadoid fishes also were present. Large striped bass generally migrate into southern waters to overwinter (Boreman & Lewis 1987) and no fish above 450 mm were sampled in winter in the UPATL region. Smaller fish (150–450 mm) overwinter in estuaries in the Upper Atlantic and the diets consisted of primarily sand shrimp, amphipods and juvenile alosid fishes.

Chesapeake–Delaware region. In the Chesapeake–Delaware region, Atlantic menhaden generally dominated the diets of fish of all sizes in most seasons (Fig. 7). Exceptions to this were smaller fish (150–600 mm) that consumed greater quantities of blue crabs, *Callinectes sapidus* (Rathbun), mysid shrimp, and anchovies in spring and summer and gizzard shad, *Dorosoma cepedianum* (Lesueur), and white perch, *Morone americana* (Gmelin), in winter. Other species of importance in the diet were the sciaenid fishes (spot, Atlantic croaker and weakfish) and blueback herring and alewives, *Alosa pseudoharengus* (Wilson), during the spring anadromous migration. Strong ontogenetic differences in the diet were not observed in fish of these size ranges, though the diet of smaller striped bass contained more small forage such as anchovies and more invertebrates such as mysid shrimp and amphipods.

North Carolina region. The absence of size-specific data for striped bass from the North Carolina region necessitated the pooling of all size classes. Menhaden was the predominant prey across all seasons, with Alosine herrings and sciaenid fishes comprising much of the remainder of the diets (Fig. 8). As with fish in the UPATL and CBDEL regions in spring, striped bass fed on anadromous herrings during their shared migrations. In the winter, striped bass preyed upon juveniles of these same herrings as they overwintered.

Seasonal patterns in diet

Several seasonal patterns in feeding were evident (Figs 6–8). During spring, Atlantic menhaden was the major constituent of the diet in most locations, though anadromous river herrings and the estuarine resident white perch and gizzard shad were also important. During the anadromous migration, striped bass encounter both the co-migrating adult river herrings as well as the resident white perch and gizzard shad. Although feeding intensity decreases during the spawning period, striped bass continue to feed

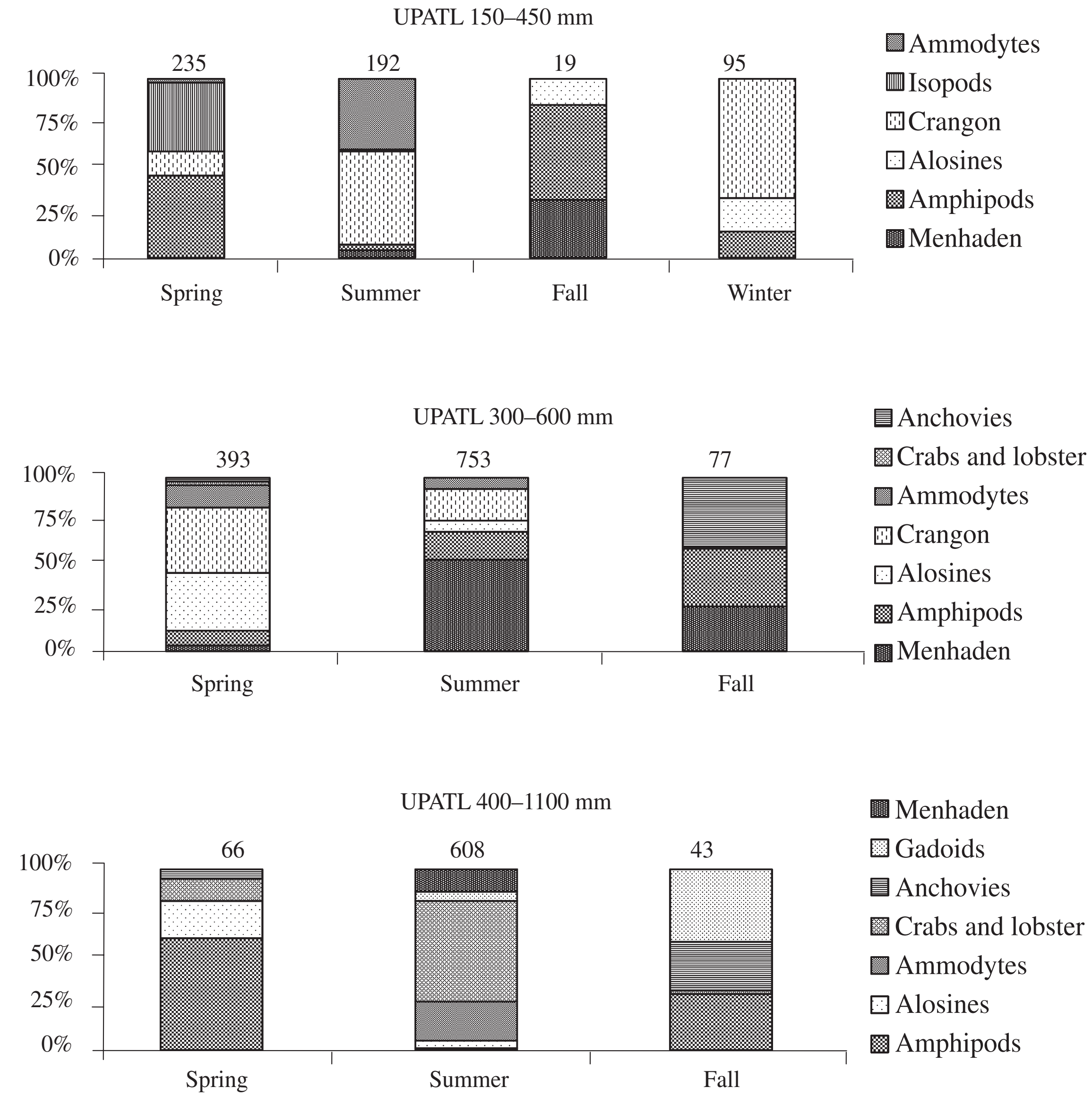

Figure 6. Diet compositions of striped bass from the Upper Atlantic region plotted by season. Numbers above bars are numbers of full stomachs. Note that overlap exists between size classes due to differential partitioning by the original authors.

throughout the migration (Trent & Hassler 1966; Walter 1999; A.S. Overton, unpublished data).

In summer, invertebrates became a larger part of the diet in all locations. During this period, the majority of samples consisted of smaller, resident striped bass with few larger fish from either UPATL or CBDEL and no large fish from NCARO. In CBDEL, blue crabs comprised over 50% of the diet for fish between 451 and 600 in summer and in the UPATL, green, *Carcinus maenas* (Linnaeus), rock, *Cancer spp*., and lady crabs, *Ovalipes ocellatus* (Herbst), and lobster, *Homarus americanus* (Milne Edwards), contributed to over 60% of the diet of similar sized fish.

The autumn feeding patterns reflected increased consumption of Atlantic menhaden, juvenile river herrings and sciaenid fishes in most locations. In autumn, YOY Atlantic menhaden, river herrings and sciaenids leave their shallow water nursery areas in the estuary and represent an abundant and accessible food source for striped bass (Hollis 1952). Striped bass migrate southward from UPATL waters towards overwintering areas in CBDEL and NCARO (Boreman & Lewis 1987). Much of the annual growth and the highest consumption rates of striped bass occur during the autumn period (Hartman & Brandt 1995b) and, in bioenergetic simula-

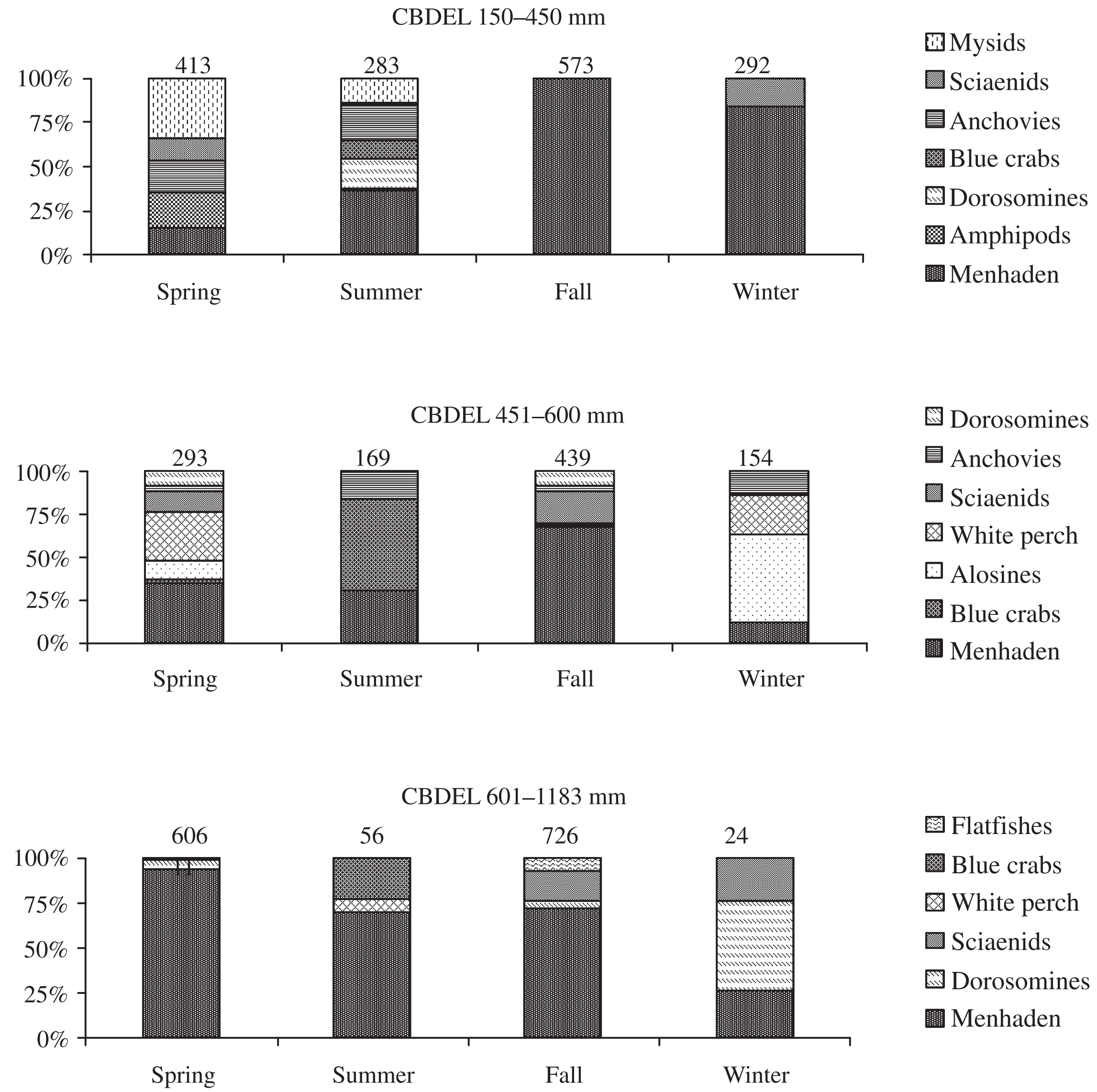

Figure 7. Diet compositions of striped bass from the Chesapeake–Delaware region by size class and season. Numbers above bars are numbers of full stomachs.

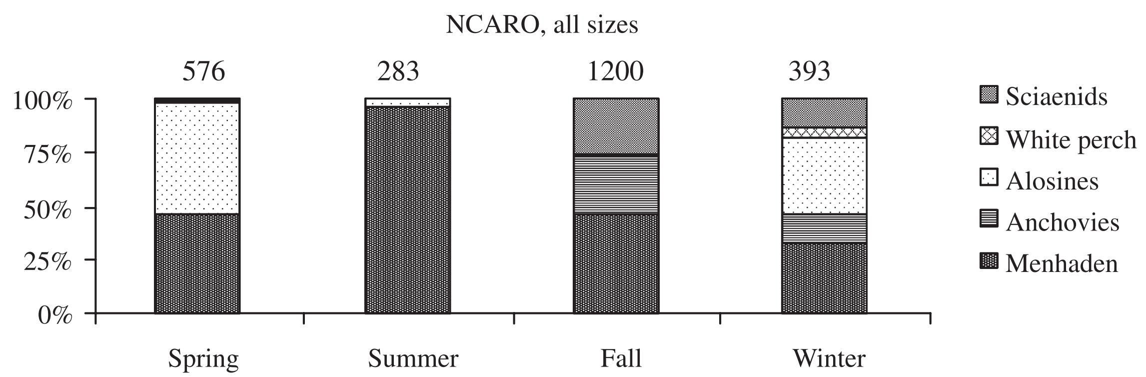

Figure 8. Diet compositions of striped bass from the North Carolina region plotted by season. Numbers above bars are numbers of full stomachs.

tions in Chesapeake Bay, growth potential peaked in October as water temperatures declined to favourable ranges and prey biomass peaked (Brandt & Kirsch 1993).

Ontogenetic changes

No definitive ontogenetic shift in the diet for fish above YOY was found. Rulifson & McKenna (1987) observed greater consumption of invertebrate prey in smaller striped bass; however, no dramatic ontogenetic shift from invertebrate to vertebrate prey was found. There is a trend of increasing prey size with increasing predator size. Larger striped bass have a greater prey-size spectrum of prey and are capable of feeding on many adult fishes. Striped bass in the 150–450 mm size range appeared to be a transitional size switching seasonally between invertebrate and vertebrate prey in relation to abundance of either prey type. In contrast, larger striped bass (600–1200 mm TL) consumed primarily piscine prey, although large fish in the UPATL region consumed crabs and lobsters during the summer.

Synthesised diet

Although there is much individual variation in migratory behaviour (Secor, Rooker, Zlokovitz & Zdanowicz 2001), an annual diet for striped bass that reflects the general migratory pattern of the species was found. Striped bass are resident within estuaries as juveniles and young adults (Merriman 1941) and, with increasing size and age, become migratory, moving northward along the Atlantic coast in the spring and southward in autumn and winter (Kohlenstein 1981; Boreman & Lewis 1987). Larger striped bass, above 600 mm, exhibit a general migratory pattern of overwintering in the coastal North Carolina region, spawning in Chesapeake Bay in spring, migrating northward to summer in the UPATL region and then returning to Chesapeake Bay in autumn (Boreman & Lewis 1987). This generalised pattern, inferred from catches and tag return data (Chapoton & Sykes 1961) allows striped bass to remain in favourable water temperatures, take advantage of latitudinal variations in the timing of peak productivity and follow the migrations of their major prey species, the menhaden. When an annual diet is constructed from this migratory pattern, striped bass feed in the spring on Atlantic menhaden and anadromous herrings in Chesapeake Bay, consume crabs, lobsters, sand eels and Atlantic menhaden in Upper Atlantic waters during summer and early autumn, then return to Chesapeake Bay in late autumn to feed upon menhaden and sciaenid fishes and overwinter in North Carolina waters where they continue to feed on menhaden and scieanid fishes.

Discussion

Methodological issues

Two problems exist in the pooling of diet data to create a standard diet composition. First, the taxonomic resolution of the diet determines how the diet can be pooled. Studies that did not resolve the diet to species level for certain prey, such as decapod crustaceans, are difficult to compare with diet studies where resolution to species level is complete. Incomplete resolution can artificially inflate the importance of pooled categories. Quantifying the diet by frequency of occurrence also presents problems when pooling two prey species into a higher category, such as combining spot and croaker into sciaenids. If both species are found exclusively of the other in the stomachs, then simply adding the $\%F$ is appropriate. If, however, the species overlap in a single stomach then adding the $\%F$ inflates the frequency of occurrence and may inflate it above 100%. In this study, a pooled $\%F$ was used, acknowledging that this may also present problems; however, it appeared to be the best method for pooling a non-additive measure such as percent frequency of occurrence for the purposes of exploring broad patterns in the diets of striped bass. In addition, the pooling of different methods of quantification presents problems when prey items may differ greatly in size or mass. For example, mysid shrimp are often present in high numbers in stomachs, yet contribute little to dietary biomass, whereas fish may not be numerically abundant but may constitute a larger percentage of the dietary biomass. When possible, compound indices were used to address this problem of methodological incompatibility. Macdonald & Green (1983) found that different methods of quantification often yield similar and redundant conclusions regarding prey importance.

Diet

From this analysis, several general themes became evident. The overall dominance of clupeid prey in the diet was the strongest trend and, in each region, size class and over all seasons. In particular, menhaden and anadromous river herrings were found in each region and contributed most to the overall diet biomass. Shared life histories and migration patterns between striped bass and several clupeids may account for their predominance in the diets. Menhaden and striped bass share similar coastal migration patterns, and Raney (1952) suggested that the migrations of striped bass may, in part, follow that of menhaden and other prey species. Striped bass also share an anadromous life history with the river herrings and this shared migration brings both species into close proximity during their spawning seasons. The dominance of clupeid prey in the diets is well documented for specific locations (Manooch 1973; Oviatt 1977; Walter 1999; Griffin 2001), and this synthesis indicates that this theme is conserved throughout the range of striped bass. Clupeids are filter-feeding, schooling fishes that, through their low trophic position and high fecundity, support large populations that, in turn, due to their importance in the diets, appear to support the population of striped bass on the East coast.

Overall, this synthesis of diet data describes several major themes in the trophic biology of striped bass, although the review does not address issues regarding interannual variability due to changes in prey availability and small spatial scale variation in the diet, both of which have an important influence on the localised diets of striped bass. The extended time period of data integrated into this study also spans dramatic changes in striped bass abundance, particularly the striped bass decline of the 1970s and 1980s and the recovery period of the 1990s. Furthermore, the broad spatial scale of this analysis provides no detail regarding habitat-specific feeding habits, which may differ from an integrated annual diet. Through the synthesis of diet studies, the coast-wide diet of striped bass, which has numerous uses as input into ecological models (Whipple *et al.* 2000) and for multi-species management, is now available. This synthesis has elucidated large-scale patterns in diet composition and provided an understanding of the coast-wide trophic biology upon which continued standardised data collection can be based.

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